

Pronounced long-term juvenation in the spawning stock of Arcto-Norwegian cod (*Gadus morhua*) and possible consequences for recruitment

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Abstract: The oldest and largest individuals are disappearing from many fish stocks worldwide as a result of overexploitation. This has been suggested to impair recruitment through decreasing the reproductive capacity of the spawners and increasing the mortality rate of the offspring. By using a time series on spawners biomass by age class for Arcto-Norwegian cod (*Gadus morhua*) from 1913–2004, I have documented pronounced changes in the spawning stock, including a trend towards younger fish, a less diverse distribution across ages, and a declining proportion of repeat spawners. Despite the total spawning stock biomass (SSB) being at similar levels now as in 1933, the mean age in the SSB has declined from 10–12.5 years to 7–8 years during the study period, and the percentage of fish of age 10 or above in the SSB has decreased from ~97% to ~10%. Contrary to earlier theoretical and experimental studies, no clear link between age structure and recruitment was found here. Recruitment to the Arcto-Norwegian cod stock may thus be more robust towards spawner juvenation than expected, possibly because of strong recruitment compensation.

Résumé : Les individus les plus âgés et les plus grands sont en train de disparaître de plusieurs stocks de poissons à l'échelle du globe à cause de la surexploitation. On croit que ce phénomène nuit au recrutement en diminuant la capacité reproductive des reproducteurs et en augmentant le taux de mortalité des rejetons. Des séries chronologiques de données sur la biomasse des reproducteurs en fonction de la classe d'âge chez des morues (*Gadus morhua*) arcto-norvégiennes de 1913 à 2004 mettent en évidence des changements dans le stock des reproducteurs, en particulier une tendance vers les poissons plus jeunes, une distribution moins diversifiée des classes d'âge et une diminution de la proportion des itéropares. Même si la biomasse totale du stock des reproducteurs (BTSR) est de même niveau actuellement qu'en 1933, l'âge moyen dans la BTSR a décliné de 10–12,5 ans à 7–8 ans, durant la période d'étude, et le pourcentage de poissons d'âge 10 ou au delà dans la BTSR est tombé d'approximativement 97 à 10 %. Contrairement à certaines études antérieures théoriques et expérimentales, la présente étude ne trouve aucun lien clair entre la structure en âges et le recrutement. Le recrutement du stock arcto-norvégien de morues peut ainsi être plus robuste vis-à-vis le rajeunissement des reproducteurs qu'on ne l'avait prévu, peut-être à cause d'un fort recrutement compensatoire.

[Traduit par la Rédaction]

Introduction

A substantial amount of literature has voiced concern about juvenation and loss of age diversity of marine fish populations. Removal of the largest individuals, decreasing the mean age as well as the age diversity of the spawning stock, is a typical consequence of the overexploitation that has taken place during the recent decades (Law 1991, 2000; Caddy and Agnew 2003). Furthermore, it is widely accepted that such a development may seriously impair recruitment (Ponomarenko 1973; Beamish et al. 2006).

Here, by means of uniquely long time series on spawners biomass by age class from 1913–2004, I document a development towards younger fish, fewer age classes, and a declining proportion of repeat spawners in the spawning population of the Arcto-Norwegian (A-N, also known as Northeast Arctic) stock of Atlantic cod (*Gadus morhua*).

Further, I consider the possible consequences of these changes for recruitment.

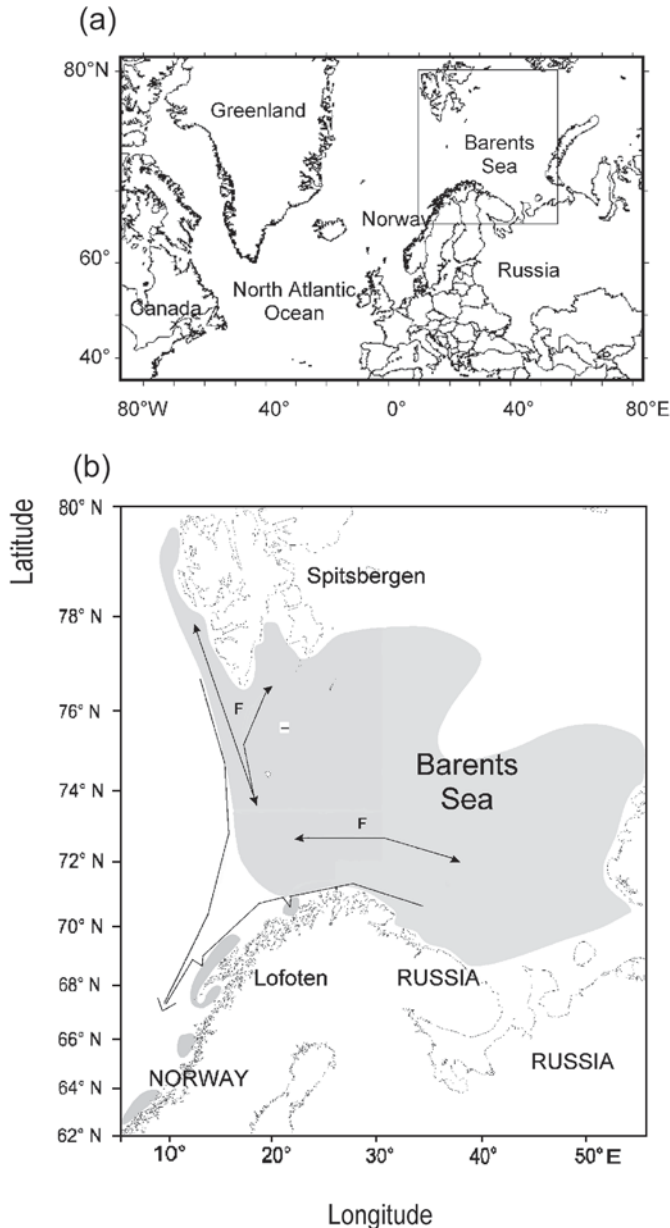
The Arcto-Norwegian cod spawn in March–May in patchy areas off mid- and northern Norway (Ellertsen et al. 1989; Fig. 1). Before they settle toward the bottom in September–November, eggs, larvae, and later juveniles follow the currents toward the north and east, drifting 600–1200 km from their spawning ground (Sundby et al. 1989). Before settlement, the cod are spread southwest of Spitsbergen and all over the southern part of the Barents Sea, an open arcto-boreal shelf sea situated off the Northeast Atlantic, north of Norway and northwestern Russia between 70°N and 80°N (Fig. 1). The age at maturation is now around 7 years for females and 6 years for males, but it was significantly higher early in the study period (Law 1991; Ajiad et al. 1999).

A number of experimental and field studies suggest that older, larger, more experienced female cod tend to have a

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Fig. 1. (a) The North Atlantic with the Barents Sea region outlined. (b) The Barents Sea and northern part of Norway showing important spawning grounds (shaded zones along the Norwegian coast) and nursery–feeding grounds (large shaded area in the Barents Sea) of Arcto-Norwegian cod (*Gadus morhua*). Open arrows indicate spawning migration, and solid single-line arrows indicate seasonal feeding migration of young fish (F). Adapted from Ottersen et al. (2006).



disproportionably higher reproductive capacity than younger, smaller recruit spawners. This applies to both A-N cod (Solemdal et al. 1995; Kjesbu et al. 1996; Marshall et al. 1998) and other stocks (Meekan and Fortier 1996; Marteinsdottir and Begg 2002; Marshall et al. 2003).

Evidence suggests that a diverse age structure in the spawning stock also may be favourable for recruitment. A population's reproductive potential could be enhanced by a heterogeneous stock composition through size- or age-

dependent differences in timing, duration, or location of spawning, ensuring that a sufficient number of eggs and larvae encounter environmentally favourable conditions. The risk of recruitment failure is reduced by spawning over a large area or a prolonged season. There is extensive documentation in support of such an effect over a broad range of stocks, including cod in Icelandic waters (Marteinsdottir and Thorarinnsson 1998) and on Georges Bank (O'Brien et al. 2003), herring (*Clupea harengus*) on the east coast of Canada (Lambert 1987, 1990), haddock (*Melanogrammus aeglefinus*) on Georges Bank (Marshall et al. 2003), and striped bass (*Morone saxatilis*) in Chesapeake Bay (Secor 2000).

The virtual population analysis (VPA; International Council for the Exploration of the Sea (ICES) 1965) based time series applied by, among others, the Arctic Fisheries Working Group of ICES, started in 1946. These data were applied in a recent paper, where we document a strengthening of the climate–recruitment relationship for A-N cod during the period 1946–2002 (Ottersen et al. 2006). A development towards a younger spawning stock with fewer age classes present was suggested to be the main mechanism, working through decreasing the stock's robustness towards environmental fluctuations.

The present paper builds on that study but focuses not on climate effects, but on changes in the spawning stock and possible consequences for recruitment. Further, by applying results from a VPA extended backwards to 1913 by Hysten (2002) and recently made available to me, I have been able to study the period from 1913–2004, a full 92 years. Here I describe the development in spawning stock biomass (SSB; the aggregated weight of mature fish in a stock) and spawners biomass by age in absolute numbers, as well as percentage of total spawning stock biomass. The temporal development of mean age and age diversity in the spawning stock is examined. I also estimate the numbers and proportion of first-, second-, and third-time or more spawners and document decadal trends, as well as interannual patterns.

Following the literature cited earlier, one would expect that recruitment to the A-N cod would be better explained by variables relating to spawning stock age and experience than by SSB alone. Consequently, I examine these links.

Material and methods

Previously published values of spawner biomass by age group from ages 3 to 13 and older (13+) as estimated by means of VPA were used. VPA is mainly based on commercial catch statistics; recent years are tuned by scientific surveys. XSA (extended survivors analysis; Shepherd 1999) was used by ICES to tune the VPA for A-N cod. Values are from ICES (2005, table 3.25) for 1946–2004 and from Hysten (2002) and K. Nedreaas (Institute of Marine Research, P.O. Box 1870 Nordnes, N-5024, Norway) for 1913–1945. Both sources give values of spawner biomass at the time of spawning, so no temporal adjustment was necessary.

Total SSB for year j is calculated as

$$(1) \quad SSB_j = \sum_{i=3}^{13+} N_i \bar{W}_i M_i$$

where N_i is number at age i , \bar{W}_i is the mean weight at age i , and M_i is the proportion of mature fish at age i (for more information, see ICES 2005). Please note that weight at age and maturity at age taken from Hylen (2002) are fixed for the period 1913–1931.

It follows that the biomass of spawners of age i in year j is

$$(2) \quad SB_{i,j} = N_{i,j} \bar{W}_i M_{i,j}$$

Because spawner biomass is given from ages 3 to 13+ for 1946–2004 and ages 3 to 15+ for 1913–1945, the values for the latter period were adjusted by defining a 13+ group as the sum of the values for the 13, 14, and 15+ groups to get a uniform time series. Age groups 3–13+ for the full period 1913–2004 are used for all further calculations.

Percent of spawning stock biomass per age i and decade d , $P_{i,d}$, was calculated as the mean percentage over all years within that decade, i.e.,

$$(3) \quad P_{i,d} = \left(\frac{1}{n} \sum_{j=1}^n SB_{i,j} / SSB_j \right) \times 100$$

I have made no attempt to correct for possible aging errors that may have been introduced during otolith reading (Campana 2001), but apply SSB values as published (ICES 2005). Regular exchanges between Russia and Norway of otoliths and age readers helped to avoid systematic differences in age reading for this stock (ICES 2003).

Following Ottersen et al. (2006), the “mean age” of the spawning population, determined for each year j separately, was estimated by calculating a spawning biomass weighted mean value added over all age groups potentially contributing to the spawning stock (age classes 3–13+):

$$(4) \quad \overline{\text{age}}_j = \frac{\sum_{i=3}^{13+} (SB_{i,j} \text{ age}_{i,j})}{\sum_{i=3}^{13+} SB_{i,j}}$$

with all fish in the 13+ group being set to age 13 because of a lack of better objective alternatives.

The Shannon diversity index (H ; Shannon 1948) is a well-known measure of species diversity described in a number of ecology textbooks, e.g., Magurran (1988). H has earlier been used to estimate the yearly diversity of the age structure of cod spawning stock abundance (Marteinsdottir and Thorarinsson 1998; Ajiad and Jakobsen 2002) or biomass (O’Brien et al. 2003). H is independent of stock size and describes both the number of cohorts in the stock and the diversity of the distribution of fish among cohorts (Marteinsdottir and Thorarinsson 1998) and is defined as

$$(5) \quad H = - \sum_{i=1}^k (p_i (\log p_i))$$

where k is the number of age groups present and p_i is the proportion in age group i of the total SSB. A large value of H thus denotes many year groups contributing equally to the SSB, whereas small values describe cases with large differences between age groups regarding contribution to the total SSB.

Assuming that mortality at age is equal for mature and immature fish, the biomass of first-time spawners was calculated for each year j as follows:

$$(6) \quad SB_{1st,j} = \sum_{a=3}^{13+} (M_{a,j} - M_{a-1,j-1}) B_{a,j}$$

where $B_{a,j} = SB_{a,j} / M_{a,j}$ is the biomass of all fish of age a at time of spawning in year j .

It follows that the biomass of repeat spawners is

$$(7) \quad SB_{2nd+,j} = SSB_j - SB_{1st,j}$$

The proportion of first-time spawners is

$$(8) \quad PSB_{1st,j} = \frac{SB_{1st,j}}{SSB_j}$$

and the proportion of repeat spawners is

$$(9) \quad PSB_{2nd+,j} = \frac{SB_{2nd+,j}}{SSB_j}$$

allowing the calculation of the biomass of second-time spawners as

$$(10) \quad SB_{2nd,j} = \sum_{a=3}^{13+} (M_{a,j} - M_{a-2,j-2}) SB_{2nd+,j}$$

and the biomass of fish having spawned three times or more as

$$(11) \quad SB_{3rd+,j} = SB_{2nd+,j} - SB_{2nd,j}$$

This gives the proportion of second-time spawners as

$$(12) \quad PSB_{2nd,j} = \frac{SB_{2nd,j}}{SSB_j}$$

and the proportion of fish having spawned three times or more as

$$(13) \quad PSB_{3rd+,j} = \frac{SB_{3rd+,j}}{SSB_j}$$

For spawners biomass, the proportion mature at age is given for ages 3 to 13+ for 1946–2004 and for ages 3 to 15+ for 1913–1945. Therefore, to make the time series uniform over the full period, in the calculations above for each year j in 1913–1945, I used the proportion mature for age group 13+ as the spawners biomass weighted mean of proportion mature at ages 13, 14, and 15+, i.e.,

$$(14) \quad M_{13+,j} = \frac{\sum_{a=13}^{15+} (SB_{a,j} M_{a,j})}{\sum_{a=13}^{15+} SB_{a,j}}$$

Recruitment to the stock is estimated by number at age 3 from VPA (VPA_3), the youngest age for which numbers are estimated by VPA for this stock. Thus, year-class strength for year i is taken as the number of 3-year-old fish in year $i + 3$. For the spawning stock data, values for 1946–2004 (1943–2001 year classes) are from ICES (2005, table 3.26), and values for 1913–1945 are from Hylen (2002).

Survival until recruitment at age 3 ($Surv_3$) is proportional to the number of recruits per spawning stock biomass, defined as

$$(15) \quad Surv_3 = VPA_3 / SSB$$

A linearised Ricker stock–recruitment model (Ricker 1954) was fitted:

$$(16) \quad VPA_3 = a SSB e^{-bSSB}$$

By taking the natural logarithms on both sides of the equation, I get

$$(17) \quad \ln(VPA_3) = \ln(a) + \ln(SSB) - bSSB \\ \Leftrightarrow \ln(VPA_3) = a' - bSSB + \ln(SSB)$$

$R_{3,res}$ is defined to be the residuals from fitting this model to our data.

Because one cannot a priori assume that the data are normally distributed, I have used nonparametric Spearman rank correlations, r_S , to express the degree of linear relation between recruitment and spawning stock related variables.

Results

The age composition of the spawning stock of A-N cod changed substantially throughout the study period (1913–2004), with older age groups being replaced by younger (Fig. 2a). Until 1951, the biomass of adult fish of age 10 and older was always above 300 000 tonnes (t), at the most, and in 1929–1930, it was above 1 000 000 t. It decreased during the late 1940s and 1950s, and since 1974, it has only been above 100 000 t in 1993–1994, most of the time being well below 50 000 t.

The change in frequency distribution of adult fish biomass between age groups is striking (Fig. 2b). It was relatively stable until the late 1940s, but since then, younger age groups have become more and more dominant. In the decades preceding World War II, about 25% of the SSB was in the age-13 and above group; since the 1980s, the decadal averages have been below 1%. Although almost 97% of this biomass was in fish of age 10 and older in 1933 and above 90% as late as 1947, it has fluctuated during the recent decade between 3% and 17%.

This development is further clarified by examining the mean age in the spawning stock. It varied between 10 and 12.5 years during the period 1913–1950 but has since then decreased by more than 3 years to 7–8 years (Fig. 3a). In reality, this change is likely to be significantly larger. In the early part of the study period, many of the fish in the 13+ group were older than 13; thus, I underestimate the mean age when I use 13 as the maximum.

The development in the number of age classes contributing to the spawning stock and the balance between them, as estimated by H , is characterized by pronounced short-term variability, particularly since the late 1960s. In addition, an increase from 1940 to the mid-1950s and a decreasing trend since is also seen (Fig. 3b).

The biomass of first-, second-, and third-time or more spawners all display a temporal development similar to that of SSB as a whole (not shown). The relative biomass has more interesting dynamics. There is a clear trend towards a

larger fraction of the spawning stock consisting of recruit spawners, a relatively constant fraction of second-time spawners and, consequently, a smaller fraction of third-time or more spawners in recent years (Fig. 4a). From being quite stable earlier, there is a pronounced increase in interannual variation in the percentage of first-time spawners from around 1960 (Fig. 4b). The development is similar for second-time spawners (not shown), whereas the proportion of fish that had spawned three times or more varies inter-annually throughout and displays a generally decreasing trend. There is a weak but statistically significant tendency towards the proportion of repeat spawners being high when SSB is high: $r_S(SSB, PSB_{2nd+}) = 0.24$ ($n = 91$, $p < 0.01$); $r_S(SSB, PSB_{3rd+}) = 0.29$ ($n = 90$, $p < 0.01$). The link between mean age in the SSB and proportion of repeat spawners is clear: $r_S(\text{age}, PSB_{2nd+}) = 0.48$ ($n = 91$, $p < 0.01$); $r_S(\text{age}, PSB_{3rd+}) = 0.59$ ($n = 90$, $p < 0.01$).

Recruitment shows pronounced year-to-year variability (Fig. 5a), the maximum value of 1 800 000 t in the 1970 year class being more than 16 times that of the minimum 112 000 t in the 1966 year class. No obvious long-term trends are seen, though. Furthermore, SSB does not explain a lot of the recruitment variability. The correlation between SSB and VPA_3 (or $\ln(SSB)$ and $\ln(VPA_3)$ as r_S measures rank correlation only) is 0.12 ($n = 89$, $p \gg 0.05$). Assuming that variables relating to the age structure of the stock might explain more of the variability in recruitment or recruitment-related variables beyond that of SSB, I calculated the following, where $Surv_3$ is, as earlier defined, recruitment per SSB and $R_{3,res}$ is residuals from a Ricker stock–recruitment model.

$$r_S(Surv_3, \overline{\text{age}}) = -0.48 \quad (n = 89, p < 0.01)$$

$$r_S(Surv_3, H) = 0.23 \quad (n = 89, p < 0.05)$$

$$r_S(Surv_3, PSB_{2nd+}) = -0.17 \quad (n = 88, p \gg 0.05)$$

$$r_S(R_{3,res}, \overline{\text{age}}) = -0.10 \quad (n = 89, p \gg 0.05)$$

$$r_S(R_{3,res}, H) = 0.05 \quad (n = 89, p \gg 0.05)$$

$$r_S(R_{3,res}, PSB_{2nd+}) = 0.00 \quad (n = 88, p \gg 0.05)$$

The correlations were similarly low if VPA_3 replaces $R_{3,res}$. With the possible exception of mean age affecting survival, the age structure of the stock, as I have parameterized it, seems to have no direct statistical link to recruitment, at least not a linear one.

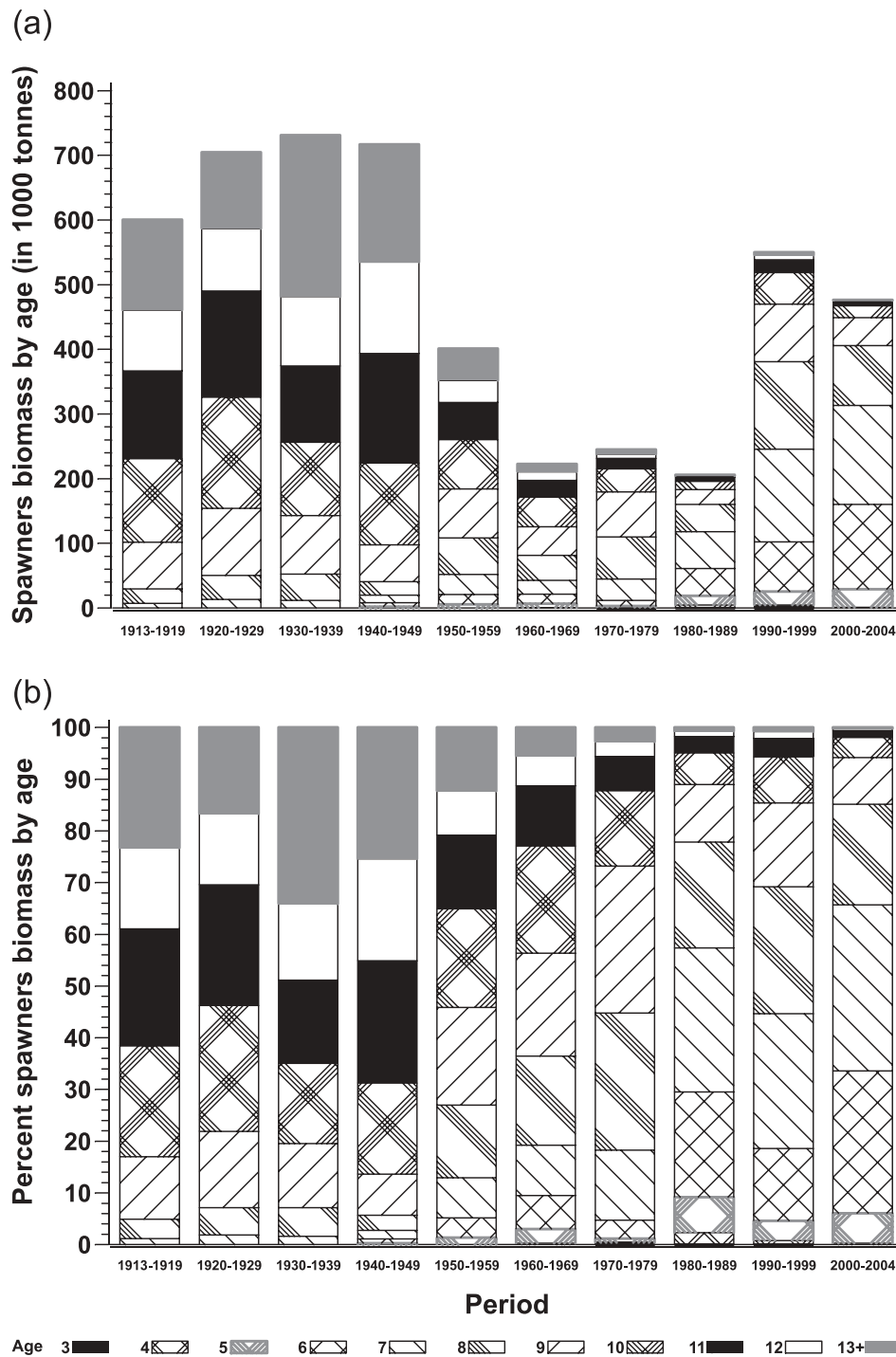
Although no easily observable temporal trend was found in recruitment, $Surv_3$ increases with time (Fig. 5b). The mean survival was 0.74 for the year classes 1913–1949, whereas for 1950–2001, it was 2.15, nearly three times as high. $\log(Surv_3)$ is always low when SSB is high, but may take on a wide range of values when SSB is low (Fig. 6). No pronounced temporal pattern was seen in the residuals from a $\log(Surv_3) - SSB$ model.

Discussion

Changes in spawning stock structure

The overall fluctuations in SSB are likely to result from a combination of biotic and abiotic environmental conditions affecting recruitment and growth, as well as changes in ex-

Fig. 2. (a) Spawning stock biomass (SSB) of Arcto-Norwegian cod (*Gadus morhua*) per year for 1913–2004 and age groups 3–13 and above (13+). (b) Decadal mean percentage of SSB by age group.

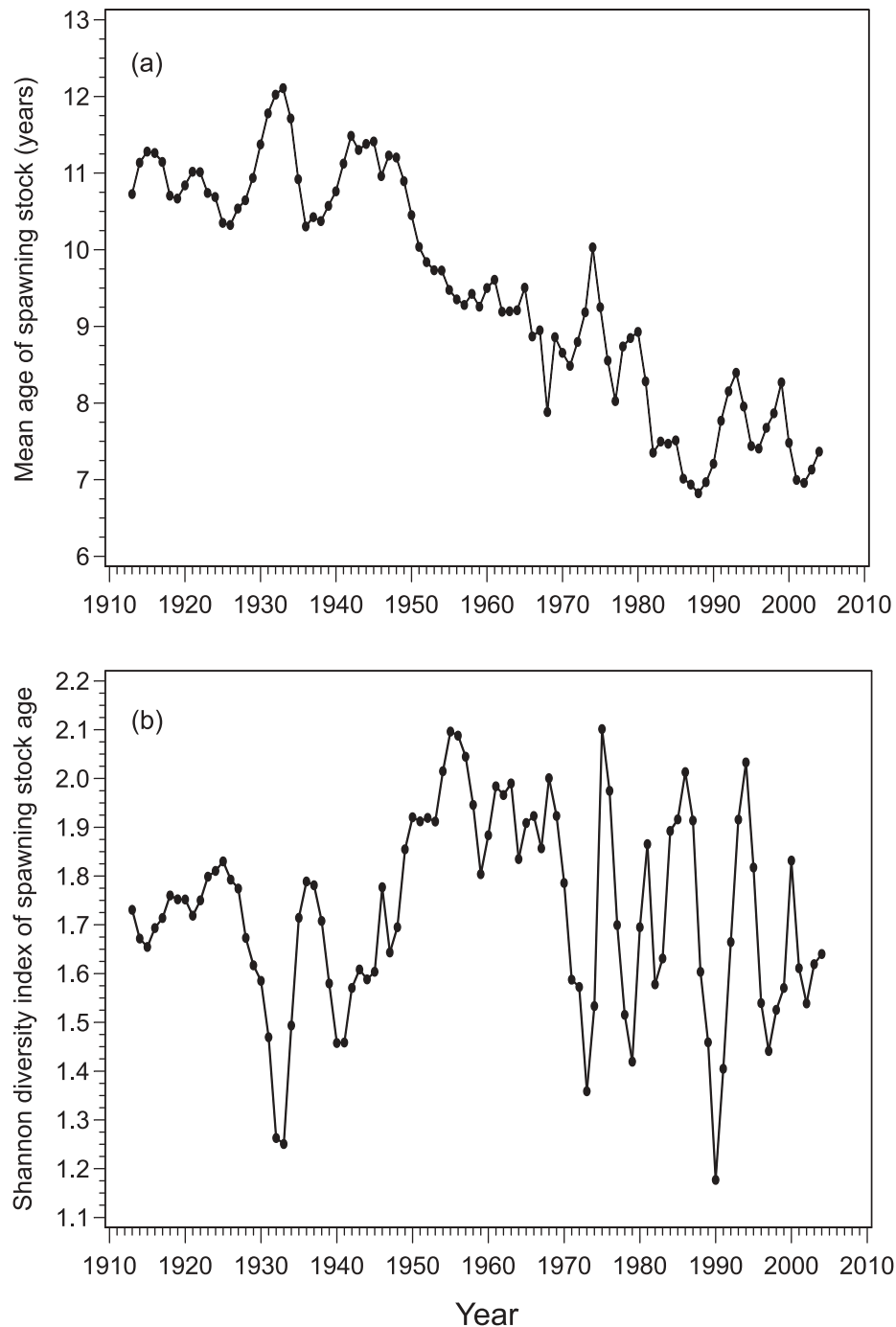


exploitation pattern. Recruitment to the A-N cod is generally assumed to be temperature-dependent, higher temperatures tending to be favourable both as a result of direct metabolic effects and through acting as a proxy for the availability of food for the early life stages of the cod (Sætersdal and Loeng 1987; Ottersen and Stenseth 2001; Ottersen et al. (2006) and references therein).

This being said, there is little doubt that the main long-term changes in SSB result from the development of the

fisheries. Until around 1920, traditional fisheries using passive gears like hand lines, long lines, and gillnets dominated (Godø 2003). These fisheries were restricted to the winter – early spring and coastal areas, targeting the spawning fish (mainly in Lofoten) and the cod feeding on capelin further north. The latter were both large immature fish and mature fish returning to the Barents Sea from their spawning grounds (Godø 2003). These Lofoten and “capelin cod” fisheries still make up a substantial fraction of the total catch,

Fig. 3. Temporal development for 1913–2004 of spawning stock biomass age properties: (a) spawners biomass weighted mean age; (b) Shannon diversity index of spawning stock biomass age distribution.

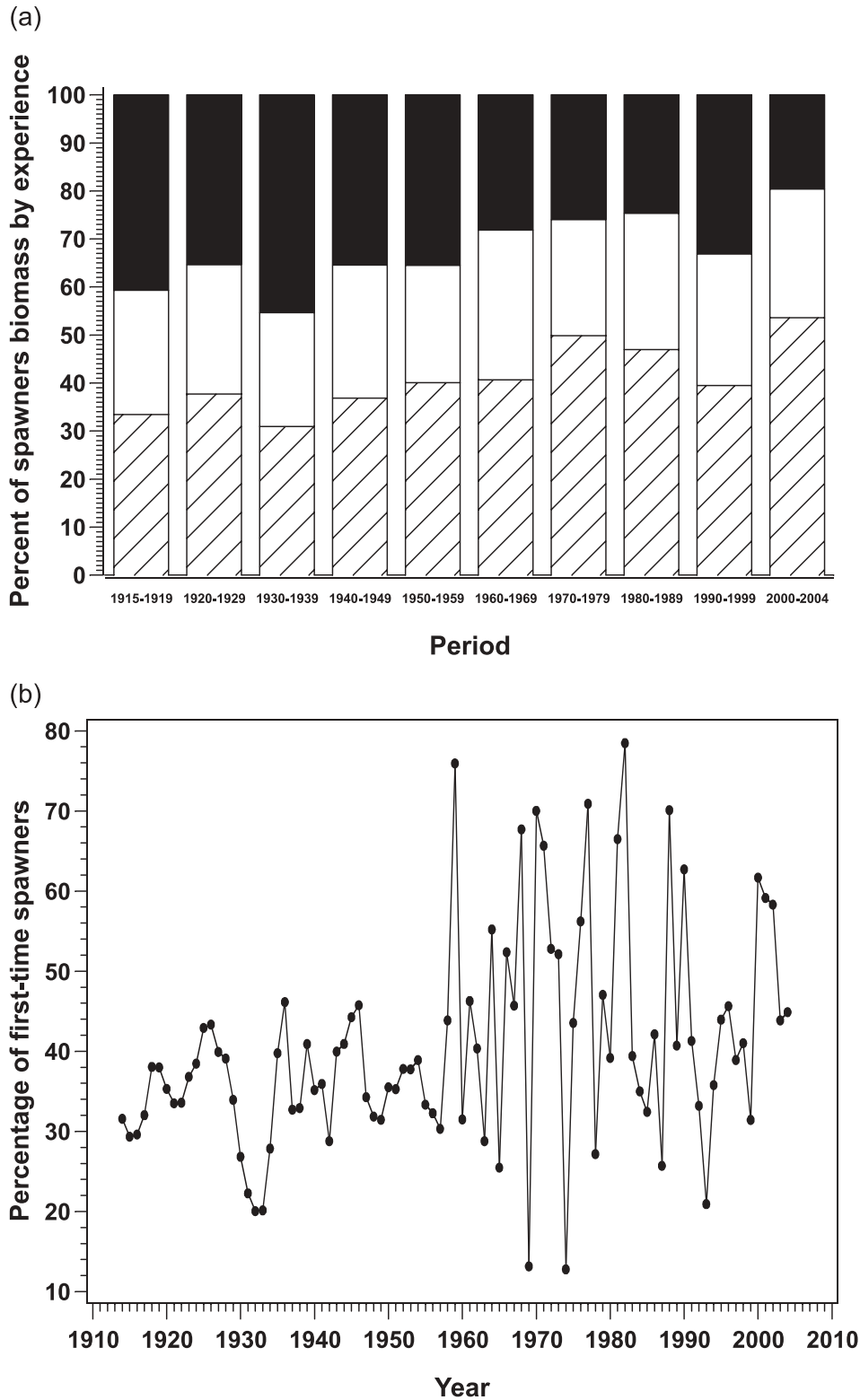


but from 1920 onwards, trawl fisheries developed, and since then, the fisheries have extended to cover most of the southern Barents Sea and now take place more or less the whole year round. This also has expanded the pattern of exploitation to include younger fish. The generally lower levels of SSB in recent years reflect that fishing mortality has increased since the late 1920s, a direct consequence of increased fishing effort (Hysten 2002). The major peak in SSB in the mid- to late 1940s followed the withdrawal of the trawling fleet during World War II, with an accompanying drop in fishing mortality, while the buildup in the early

1990s followed strict quota regulations introduced in 1987–1988 (Hysten 2002).

A pronounced reduction of older fish in the spawning stock has taken place, both in absolute numbers and relative to the total SSB. This confirms a development observed already by Sætersdal and Hysten (1964), cited by Nakken (1994), who were concerned about the catch of old and large cod decreasing relative to that of younger and smaller fish. In light of the extensive degree of change in the age structure of the stock revealed here, the reduction in mean age at the time of Sætersdal and Hysten (1964) seems quite moder-

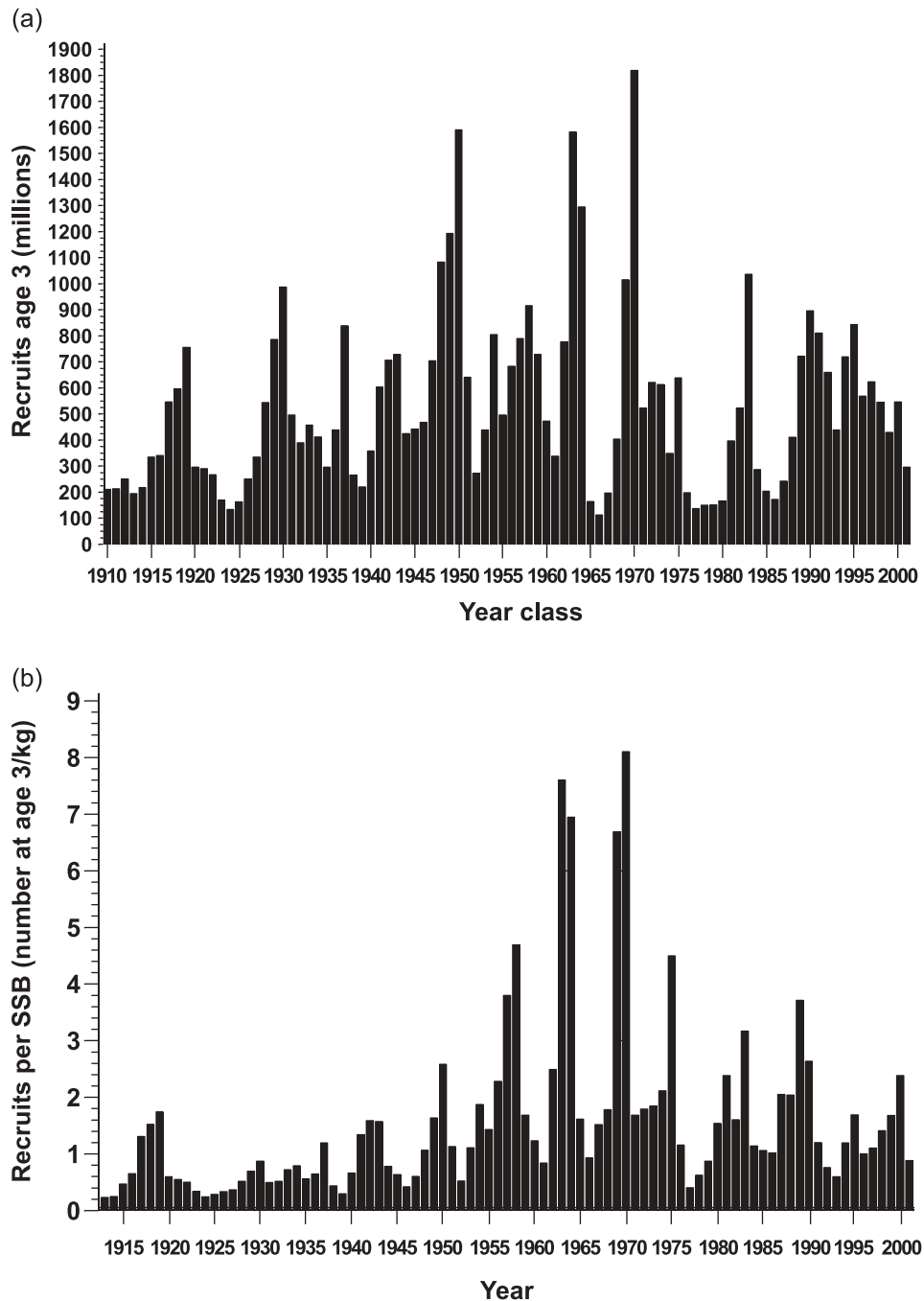
Fig. 4. Temporal development of spawning stock biomass (SSB) according to spawning experience. (a) Decadal percentage of biomass of first-time (hatched bars), second-time (open bars), and third-time or more (solid bars) spawners in the SSB. Time series begins in 1915 as estimation of third-time or more spawners depends on values from the two previous years. (b) Time series of percentage of biomass of first-time spawners in SSB.



ate. However, although the decline in mean age was relatively gradual and continuous, other changes were more abrupt and detectable earlier. Although more than 90% of

the SSB was in spawners of age 10 or older in 1947, the value for 2002 was 2.5%. A large part of this dramatic change had taken place already during the late 1940s and

Fig. 5. Time series of (a) number of recruits to the Arcto-Norwegian cod (*Gadus morhua*) stock at age 3 for the 1910–2001 year classes and (b) number of recruits at age 3 per spawning stock biomass (SSB, kg) for 1913–2001 (survival).



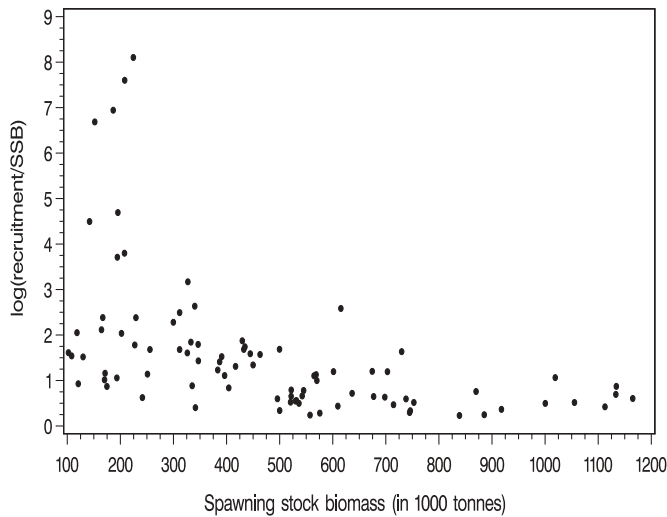
early 1950s (Ottersen et al. 2006). The trend in numbers of age-10+ fish is similarly dramatic. In the early 1990s, the abundance of cod older than 10 years had decreased to 1% of that in the late 1940s (Nilssen et al. 1994).

The severe juvenation in the spawning stock of A-N cod is a combined effect of the overall increase in fishing effort and the switch towards trawling. Fishers will naturally target fish of the most profitable size, and this tends to be relatively large individuals. In the case of the A-N cod, different age groups are distributed differently geographically in large parts of the year, making age- and size-selective fishing easier. Furthermore, trawl nets remove larger fish and let the

smaller fish through, a tendency enhanced by the enforcement of minimum mesh width. The bottom line, though, is that with the levels of fishing mortality seen through most of the last 50 years for both large and smaller fish, very few fish have a chance to remain long enough in the sea to become old. Law (1991) estimated that before the development of distant water trawlers, an immature A-N cod had a chance of roughly 40% of surviving from ages 3 to 8 compared with around 2% now.

Such a development is not unique to this stock or species. The age composition of most Atlantic cod stocks is currently strongly biased towards young fish, and it is a general ten-

Fig. 6. Spawning stock biomass (SSB) versus $\log(\text{number of recruits at age } 3/\text{SSB})$ (survival) for 1913–2001.



dency that fisheries selectively remove the larger, older individuals (Hutchings and Myers 1993; Caddy and Agnew 2003). Thus, a younger spawning stock has become a well-known phenomenon for long-lived fish in many parts of the world (Law 1991; Longhurst 2002).

My analyses are strictly based on numbers and biomass at age; however, reproductive traits such as maturity and fecundity typically depend more on length than age (Marshall et al. 2003) and hard evidence for age per se influencing fecundity or recruitment is rare (but see Berkeley et al. 2004; Rose 1993). Unfortunately, the data necessary to conduct a length-based analysis (number at length, weight at length, and maturity at length) are not available for A-N cod earlier than 1946. However, the development in mean length in the A-N spawning stock roughly paralleled that of mean age for 1946–2002 (Ottersen et al. 2006). The only significant difference was that of age dropping off more rapidly than length around 1950, which could possibly have resulted from an increase in length at age following release of density-dependent restrictions on growth caused by strongly intensified fishing pressure after the end of World War II (Ottersen et al. 2006).

I show that the proportion of SSB consisting of first-time spawners has increased from somewhat above 30% to over 50% during the study period. This must not be confused with the proportion of the number of first-time spawners in the spawning population. This fraction is naturally higher as one big repeat spawner may weigh more than several first-time spawners. During much of the period after World War II, the numbers of first-time spawners has been 60%–80% of the total numbers in the spawning stock (Jørgensen 1990; Godø 2003). The reduced proportion of repeat spawners may seem to follow naturally from the pronounced decrease seen in biomass of old spawners relative to younger, but the latter need not necessarily imply the former. Spawner biomass by age is a product of number at age, maturity at age, and weight at age. The observed changes in A-N cod are mainly an effect of a disproportional reduction in number at age of older fish (ICES 2005, table 3.23). However, the

temporal development of the proportion of first-time versus repeat spawners may be counterbalanced by earlier maturation, because increased exploitation works towards reducing age at first spawning, both by growth being enhanced by reduction in density-dependent competition (Jørgensen 1990) and by inducing strong selection pressure for early maturation (Heino et al. 2002). Indeed, the age of 50% maturity has decreased distinctly from between 9 and 11 years in the 1920s to 1950s (Law 1991) to approximately 7 years for females and just above 6 years for males during 1989–1997 (Ajiad et al. 1999). To a certain degree, this explains why the reduction in the proportion of repeat spawners is quite moderate for this stock compared with the decrease in the proportion of older fish. Still, the correlation between mean age and proportion of repeat spawners is high, which, to a large degree, reflects the mutual temporal trend from high towards lower values.

Age diversity, as represented by H , might be expected to also decline as older age groups are removed from the stock, and there has been a trend in that direction since the mid-1950s. However, following the above, this has partly been compensated for by younger age groups being introduced. Actually, some of the lowest values of H occurred in 1932–1933 when the mean age was at its very highest, whereas H was high in 1987 when both SSB and mean age were close to record low values.

When studying long biological time series, there is more often than not the challenge that the underlying data are not uniform in time, as is the case here. The annual sampling for age determination was based on scales prior to 1932 and on otoliths from that year onwards (Hysten 2002). Hysten (2002) explained the estimation of age composition for the earlier years as follows: “In the 1920s and early 1930s, age determinations of mature fish indicated a lower frequency of older fish in scale samples than in otolith samples. Misclassification of age in scale samples of immature cod was assumed to be of minor importance. To overcome the misclassification of age in mature fish, a scale-age/otolith-age ‘key’ was applied to scale-age compositions of mature fish. These annual converted age compositions together with the scale-age composition of immature cod for 1913–1929 were used to establish total annual catch in numbers at age by years.” There is no obvious reason why this procedure should cause any systematic upward bias in estimated numbers of older fish.

Of possible importance for this study is also the fact that weight and the proportion of fish mature at a given age was fixed for the period 1913–1931. This implies that the inter-annual dynamics in spawners biomass at age is determined solely by changes in numbers at age for this first period. However, there is no obvious change in SSB, H , or mean age dynamics around 1932. The increase in short-term variability observed in H since the late 1960s may be affected by dynamics in weight at age, as well as number. However, it seems likely that the low spawners biomass in all age groups during much of that period is the real source of the increased volatility in H . Similarly, it also seems highly probable that the switch from a relatively stable proportion of first- and second-time spawners in the SSB to high amplitude changes from year to year during 1960–1990 originates in the predominantly low spawners biomass.

To be able to estimate the proportion of first-time versus repeat spawners, I assumed that mortality is equal for mature and immature fish of the same age, in accordance with the practice of the ICES Arctic Fisheries Working Group. However, the spatial distribution of the age groups closest to maturation depends more on maturation status than age during the spawning season in winter. Mature fish will be located further south than immature fish and, as mentioned earlier, targeted by the fisheries on the spawning grounds, in particular around Lofoten (Godø 2003). Large, immature fish, as well as mature fish, will be targeted by the “capelin cod” fisheries. Fishing mortality during winter may thus be slightly higher for mature fish than for immature fish of the same age. The effect of assuming too low a mortality for the mature fish versus the immature fish would be an underestimation of the proportion of first-time versus repeat spawners. However, there are no indications that this has had a major influence on my results.

Links between spawning stock structure and recruitment

Contrary to what I had expected, my results show little connection between recruitment and variables related to age and experience. In fact, $Surv_3$ is negatively correlated with mean age. Although this relationship seems to be statistically significant, it should not be trusted blindly. The p values have not been adjusted for possible autocorrelations in the time series. The correlation may thus arise from the decreasing trend in mean age and the increasing trend in $Surv_3$ rather than from a common pattern in interannual fluctuations, and there may not be any causal relationship.

If we do accept that $Surv_3$ decreases with higher mean age, it strengthens my other results in indicating that older A-N cod may not be as valuable spawners as the literature suggests. In particular, I am not able to confirm the results of Ponomarenko (1973). He found negative correlations between recruitment measured as the number of cod of ages 1+ and 2+, respectively, caught per hour of trawling in the southern Barents Sea and the percentage of mature cod that were first-time spawners (taken simply as age groups 6–12). The contradiction is not explained by his study period being restricted to 1947–1966, as for these years, my correlation between $Surv_3$ and mean age is negative, i.e., the opposite of that found by Ponomarenko (1973), and between $R_{3,res}$ and PSB_{2nd+} is near 0. It may seem as though there are serious discrepancies between the data used by Ponomarenko (1973) and the VPA data of Hysten (2002) that I use. If the assumption of Ponomarenko (1973) of all fish of ages 6–12 being first-time spawners is correct, then only around 5%, on average, of the SSB belongs to repeat spawners in the 1960s according to the VPA. The pronounced fluctuations in recruitment in this decade are then unlikely to be due to variations in the proportion of first-time versus repeat spawners as he argued. However, age of 50% maturity was likely between 9 and 11 years in the 1920s–1950s (Law 1991) and has since decreased substantially (Ajiad et al. 1999).

The experimental work on A-N cod does not conclude that older cod necessarily are the better spawners, but rather that recruit spawners are inferior to second- or third-time spawners (Kjesbu et al. 1996). From this and my results, one

might speculate that there exists an optimal age or spawning status window so that too young and inexperienced cod and too old cod contribute less to recruitment than those in between. This should show up as a parabolic relationship between mean age and recruitment–survival. Visual inspection reveals that the 7 years with highest survival indeed occurred at an intermediate mean age in the SSB, between 8.5 and 9.5 years, and also that the highest values of recruitment arose at intermediate values of mean age. However, these results must be considered as indicative, and nonlinear statistical modeling (e.g., general additive modeling (GAM)) should be undertaken before more can be said about their reliability. Also, somewhat contrary to this, both $r_S(Surv_3, PSB_{2nd+})$ and $r_S(R_{3,res}, PSB_{2nd+})$ are nonsignificantly different from 0.

There is little literature on reduced fecundity with age for cod, but ovarian senescence has been shown for a few specimens (Wiles 1969; Rideout and Burton 2000). For North Sea herring, a decline in spawning capacity at old age has been described at the population level. In this stock, the proportion of ovary weight to total weight was shown to decline in fish older than 5 years and, in particular, in those older than 7 (several papers from 1940–1961 cited by Nash and Dickey-Collas (2005)).

One plausible explanation for the unexpected weak connection between changes in spawning stock age composition and recruitment for A-N cod may be increasing juvenile survival rate. Thus, decreasing mean age and age diversity may indeed have led to reduced total egg deposition over time, but this has been masked in the data on recruitment at age 3. The low values of $Surv_3$ that I found early in the study period and the following threefold increase could be a result of decreasing competition. My data only provides suggestive evidence for very strong recruitment compensation for A-N cod, although I show that high or intermediate values of $Surv_3$ only occur when SSB is low. The steepness of stock–recruitment relationships has earlier been studied more generally in a meta-analysis and (or) Bayesian context and strong recruitment compensation was found (Myers 2001; Myers et al. 2001; He et al. 2006).

To conclude, pronounced changes in the age composition of the spawning stock of A-N cod have taken place since early in the 20th century. The fish have become substantially younger, the distribution across ages less diverse, and the proportion of repeat spawners smaller. Theoretical foundation and experimental studies on this stock and time series based results for other species and cod stocks document negative effects on recruitment of a development of this kind. Still, I have not been able to prove any such systematic effects here. Seemingly, recruitment to this stock, at least up until now, is robust towards even strong fisheries-induced age changes in spawning stock age composition. The reason may be strong recruitment compensation, i.e., increased juvenile survival rate due to reduced prerecruitment competition.

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References

- Ajiad, A., and Jakobsen, T. 2002. Incorporating age diversity index and temperature in the stock–recruitment relationship of North-east Arctic cod. Working Document 3 to Report of the Arctic Fisheries Working Group. ICES (Int. Counc. Explor. Sea) CM 2002/ACFM:18. pp. 418–424.
- Ajiad, A., Jakobsen, T., and Nakken, O. 1999. Sexual difference in maturation of Northeast Arctic cod. *J. Northw. Atl. Fish. Sci.* **25**: 1–15.
- Beamish, R.J., McFarlane, G.A., and Benson, A. 2006. Longevity overfishing. *Progr. Oceanogr.* **68**: 289–302.
- Berkeley, S., Chapman, C., and Sogard, S. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, **85**(5): 1258–1264.
- Caddy, J.F., and Agnew, D. 2003. A summary of global stock recovery plans for marine organisms, including indicative information on the time to recovery and associated regime changes that may affect recruitment and recovery success. ICES (Int. Counc. Explor. Sea) CM 2003/U:08.
- Campana, S.E. 2001. Accuracy, precision, and quality control in age determination, including a review of use and abuse of age validation methods. *J. Fish Biol.* **59**: 197–242.
- Ellertsen, B., Fossum, P., Solemdal, P., and Sundby, S. 1989. Relation between temperature and survival of eggs and first-feeding larvae of Northeast Arctic cod (*Gadus morhua* L.). *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **191**: 209–219.
- Godø, O.R. 2003. Fluctuation in stock properties of north-east Arctic cod related to long-term environmental changes. *Fish Fish. Ser.* **4**: 121–137.
- He, X., Mangel, M., and MacCall, A. 2006. A prior for steepness in stock–recruitment relationships, based on an evolutionary persistence principle. *Fish. Bull.* **104**(3): 428–433.
- Heino, M., Dieckmann, U., and Godø, O.R. 2002. Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, **56**: 669–678.
- Hutchings, J., and Myers, R. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **50**: 2468–2474.
- Hysten, A. 2002. Fluctuations in abundance of Northeast Arctic cod during the 20th century. ICES (Int. Counc. Explor. Sea) Mar. Sci. Symp. **215**: 543–550.
- International Council for the Exploration of the Sea. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report of Meeting in Hamburg 18–23 January 1965. ICES (Int. Counc. Explor. Sea) Group Ref. Rep. Ser. A, **16**: 1–60.
- International Council for the Exploration of the Sea. 2003. Report of the Arctic Fisheries Working Group. ICES (Int. Counc. Explor. Sea) CM 2003/ACFM:22.
- International Council for the Exploration of the Sea. 2005. Report of the Arctic Fisheries Working Group. ICES (Int. Counc. Explor. Sea) CM 2005/ACFM:20.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *J. Cons. Int. Explor. Mer*, **46**: 235–248.
- Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **53**(3): 610–620.
- Lambert, T.C. 1987. Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. *Mar. Ecol. Prog. Ser.* **39**: 209–220.
- Lambert, T.C. 1990. The effect of population structure on recruitment in herring. *J. Cons. Perm. Int. Explor. Mer*, **47**: 249–255.
- Law, R. 1991. Fishing in evolutionary waters. *New Scientist*, 2 March 1991: 35–37.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* **57**(3): 659–668.
- Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. *Fish. Res.* **56**: 125–131.
- Magurran, A.E. 1988. Ecological diversity and its measurement. Croom Helm Limited, London, UK.
- Marshall, C.T., Kjesby, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, O. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Can. J. Fish. Aquat. Sci.* **55**(7): 1766–1783.
- Marshall, C.T., O'Brien, L., Tomkiewicz, J., Köster, F.W., Kraus, G., Marteinsdottir, G., Morgan, M.J., Saborido-Rey, F., Blanchard, J.L., Secor, D.H., Wright, P.J., Mukhina, N.V., and Bjørnson, H. 2003. Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. *J. Northw. Atl. Fish. Sci.* **33**: 161–190.
- Marteinsdottir, G., and Begg, G.A. 2002. Essential relationships incorporating the influence of age, size, and condition on variables required for estimation of reproductive potential in Atlantic cod, *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **235**: 235–256.
- Marteinsdottir, G., and Thorarinnsson, K. 1998. Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. *Can. J. Fish. Aquat. Sci.* **55**: 1372–1377.
- Meekan, M.G., and Fortier, L. 1996. Selection for fast growth during the larval life of Atlantic cod, *Gadus morhua*, on the Scotian Shelf. *Mar. Ecol. Prog. Ser.* **137**: 25–37.
- Myers, R.A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES J. Mar. Sci.* **58**: 937–951.
- Myers, R.A., MacKenzie, B., Bowen, K., and Barrowman, N. 2001. What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. *Can. J. Fish. Aquat. Sci.* **58**: 1464–1476.
- Nakken, O. 1994. Trends and fluctuations in the Arcto-Norwegian cod stock. *ICES Mar. Sci. Symp.* **198**: 212–228.
- Nash, R.D.M., and Dickey-Collas, M. 2005. The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (*Clupea harengus* L.). *Fish. Oceanogr.* **14**(4): 279–291.
- Nilssen, E.M., Pedersen, T., Hopkins, C.C.E., Thyholdt, K., and Pope, J.G. 1994. Recruitment variability and growth of Northeast Arctic cod: influence of physical environment, demography, and predator–prey energetics. *ICES Mar. Sci. Symp.* **198**: 449–470.
- O'Brien, L., Rago, P.J., Lough, R.G., and Berrien, P. 2003. Incorporating early-life history parameters in the estimation of the stock–recruitment relationship of Georges Bank cod (*Gadus morhua*). *J. Northw. Atl. Fish. Sci.* **33**: 191–205.
- Ottersen, G., and Stenseth, N.C. 2001. Atlantic climate governs oceanographic and ecological variability in the Barents Sea. *Limnol. Oceanogr.* **46**(7): 1774–1780.
- Ottersen, G., Hjermann, D., and Stenseth, N.C. 2006. Changes in spawning stock structure strengthens the link between climate

- and recruitment in a heavily fished cod stock. *Fish. Oceanogr.* **15**(3): 230–243.
- Ponomarenko, V.P. 1973. On a probable relation between age composition of spawning stock and abundance of the year classes of cod in the Barents Sea. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **164**: 69–72.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* **11**: 559–623.
- Rideout, R.M., and Burton, M.P.M. 2000. Peculiarities in ovarian structure leading to multiple-year delays in oogenesis and possible senescence in Atlantic cod, *Gadus morhua* L. *Can. J. Zool.* **78**(10): 1840–1844.
- Rose, G.A. 1993. Cod spawning on a migration highway in the northwest Atlantic. *Nature (London)*, **366**: 458–461.
- Secor, D.H. 2000. Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake Bay striped bass. *ICES J. Mar. Sci.* **57**: 403–411.
- Shannon, C.E. 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* **27**: 379–423.
- Shepherd, J. 1999. Extended survivors analysis: an improved method for the analysis of catch-at-age data and abundance indices. *ICES J. Mar. Sci.* **56**: 584–591.
- Solemdal, P., Kjesbu, O.S., and Fonn, M. 1995. Egg mortality in recruit-, and repeat-spawning cod — an experimental study. *ICES (Int. Counc. Explor. Sea) CM 1995/G:35*.
- Sundby, S., Bjørke, H., Soldal, A.V., and Olsen, S. 1989. Mortality rates during the early life stages and year class strength of the Arcto-Norwegian cod (*Gadus morhua* L.). *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **191**: 351–358.
- Sættersdal, G., and Hysten, A. 1964. The decline of the skrei fisheries. *Fiskeridir. Skr. Ser. Havunders.* **13**(7): 56–69.
- Sættersdal, G., and Loeng, H. 1987. Ecological adaptation of reproduction in Northeast Arctic cod. *Fish. Res.* **5**: 253–270.
- Wiles, M. 1969. Fibrous and cystic lesions in the ovaries of aged Atlantic cod (*Gadus morhua*): a preliminary report. *J. Fish. Res. Board Can.* **26**: 3242–3246.